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16. ABSTRACT

This chapter focuses on physical organism-sediment relations that are of potential value in predicting the physical properties of sediments and the transport fates of fine-grained sediments and their associated contaminants. Generalizations are made about how early and late successional stages influence the physical properties of sediments--some of the cause-and-effect relationships are well known, while others remain speculative. A few promising techniques and approaches for future work are discussed.

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by

Donald C. Rhoads and Larry F. Boyer
Department of Geology and Geophysics
Yale University
P. O. Box 6666
New Haven, CT 06511

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EPA Project Officer
Thomas W. Duke

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Chapter One

The Effects of Marine Benthos on Physical Properties of Sediments: A Successional Perspective

Donald C. Rhoads and Larry F. Boyer*

1. Introduction

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References

*Donald C. Rhoads and Larry F. Boyer
Department of Geology and Geophysics
Yale University
P.O.Box 6666
New Haven, CT. 06511

1. Introduction

The effects of benthic organisms on the physical properties of granular substrata are well documented. The range of effects have been presented in Moore, 1931, 1939; Schwarz, 1932; Dapples, 1942; Moore and Scruton, 1957; McMaster, 1967; Rhoads, 1974; Rowe, 1974; Powell, 1974; Richards and Park, 1976; Myers, 1977; Self and Jumars, 1978; Lee and Swartz, 1980; Carney, in press. These papers relate the effects of benthic species to changes in grain size, sorting, fabric, water content, compaction, shear strength and bottom stability. Those autecologic parameters which appear to be most highly correlated with physical modifications of sediments include: method of feeding, feeding selectivity, feeding level relative to the sediment-water interface, degree of mobility, organism size and population density, burrowing depth, and, if the organism is a tube-dweller, the density, spacing and length of tubes.

The influence of most invertebrate benthos on the biological benthic boundary layer* is limited to a relatively small vertical zone, i.e., from a few centimeters above the sediment surface to a few decimeters below the bottom. Important exceptions exist to this generalization, most notably shrimp that burrow to depths of 3 to 4 meters (Pemberton, Risk, and Buckley, 1976; Meyers, 1979) and certain fish that can burrow to depths of 60-70 cm (Atkinson and Pullin, 1976).

In view of the generally surficial effects of benthos on the physical properties of sediments, why study this phenomenon? Our interest in the upper few centimeters of sediment is based on the fact that the interface

is both biologically active and chemically reactive. The physical properties of sediments, as controlled by biological processes, may have a major effect on sedimentation, sediment transport, nutrient regeneration, and the fates and historical records of radiochemical species, pollutants and fossils. Biology, chemistry, and sediments are coupled through the process of bioturbation, involving the transport of particles, as well as pumping water into, and out of, the bottom. Aller (1978) has reviewed the literature on bioturbation, and makes the observation that water pumping is about 100 times greater (on a weight to weight basis) than particle bioturbation. We will see that both fluid and particle bioturbation can affect the physical properties of sediments.

The dispersal or concentration of potentially harmful environmental contaminants may be controlled by the interactions of both particulate and dissolved pollutants with the seafloor. The way a particular benthic organism or suites of benthic organisms bioturbate, or otherwise process the seafloor, can determine if a pollutant is entrapped or mixed into the bottom or alternatively, transported and dispersed (e.g. Phelps, 1967; Haven and Morales-Alamo, 1969; Swartz and Lee, 1980; Lee and Swartz, 1980; Berger and Heath, 1968, Hanor and Marshall, 1971).

A small but increasing body of data indicates that the response of sediments to fluid shear stress is significantly affected by their biological components. Plants and invertebrates are known to trap and bind sediments or promote sedimentation (Ginsburg and Lowenstam, 1958; Fager, 1964; Newman, Gebelein, and Scoffin, 1970; Marshall and Lucas, 1970; Scoffin, 1970; Lynch and Harrison, 1970; Holland, Zingmark, and Dean, 1974; Rhoads, Yingst, and Ullman, 1978; Yingst and Rhoads, 1978; Boyer, 1980; Nowell et al. 1981; and Eckman et al., in press). Sediments

can also become destabilized by organisms relative to azoic or bound conditions (Rhoads and Young, 1970; Southard, et al., 1975, Young, 1975; Young and Southard, 1978; Rhoads, Yingst and Ullman, 1978; Yingst and Rhoads, 1978; Boyer, 1980; Nowell et al., 1981, Eckman et al., in press; Grant, Boyer and Sanford, 1982).

It is the purpose of this paper to focus on those physical organism-sediment relations which are of potential value in predicting the physical properties of sediments and the transport fates of fine-grained sediments and their associated contaminants. We will limit our discussion primarily to macrofaunal effects on subtidal muds. The geochemical aspects of this problem are covered in chapter 2 of this volume. We also direct the reader to an excellent recent review of biodepositional and bioturbational effects on the distribution of pollutants in sediments (Lee and Swartz, 1980). We will not cover biogenic rate processes here (see Aller, 1978; and Lee and Swartz, 1980. Rather, our contribution will focus on how organism-sediment relations develop during ecological succession of the seafloor.* Generalizations will be made about how early and late successional stages influence the physical properties of sediments--some of the cause and effect relationships are well known, while others remain speculative. The successional paradigm for interpreting organism-sediment relations is new, and therefore, poorly tested. New kinds of measurements and observational techniques will be required to explore and test this model. We will offer a few promising techniques and approaches which we feel are necessary for conducting future work.

2. Ecological Succession and Organism-Sediment Relations

Until recently, methods of describing bottom communities and their relationships to sediments followed, more-or-less, the procedures outlined by C. G. Joh. Petersen (1913) and popularized by G. Thorson (1957). The classical Danish method of defining benthic communities consists of identifying characterizing species. Characterizing species are those which are temporally and spatially persistent, dominate in biomass, and have relatively long life spans. These criteria select for "equilibrium" species which live on parts of the seafloor where physical disturbance is uncommon. Early organism-sediment work was also done from this "steady-state" point of view. In addition, much of this early work was limited to the sedimentary effects of individuals of a species or single species populations (e.g. Crozier, 1918; Dapples, 1942; Rhoads, 1966; and Gordon, 1966). A notable exception to this generalization is the early German work in the North Sea where the effects of whole faunas on sediments were considered (see Schafer, 1972).

A more ecologically realistic concept of benthic communities was proposed by Johnson (1972), who suggested that a benthic community is a temporal and spatial mosaic, "parts of which are at different levels of succession...in this view the community is a collection of relics of former disasters". This successional perspective has its origin in plant ecology as popularized by Clements (1916).

Subsequent experimental and field work by McCall, 1977; Myers, 1977a, 1977b; Pearson and Rosenberg, 1978; Rhoads, Aller and Goldhaber, 1977; Wolff, Sandee, and DeWolf, 1977; Santos and Bloom, 1980; and Santos and Simon, 1980, helped to define the taxonomic and functional structure of

these "temporal mosaics". This dynamic approach to community structure suggests that earlier work on sub-tidal organism-sediment relations be reevaluated in terms of a successional paradigm, and that future work test the validity of these successional dynamics.

Figure 1 depicts organism-sediment relations as they develop during succession of a subtidal granular bottom. Most of the information about this successional pattern comes from mud bottoms (e.g. McCall, 1977; Pearson and Rosenberg, 1978; Rhoads, Yingst, and McCall, 1978; and Rhoads, Aller, and Goldhaber, 1977), but major qualitative features of this succession are apparently also shared with sand-dwelling faunas (e.g. Myers, 1977a,1977b).

2.1 Pioneering Stages

Pioneering stages usually occur nearshore, above the mean shoaling depth of storm waves. Disturbance assemblages may, however, be found at any water depth--even in abyssal trenches (Jumars and Hessler, 1976), and in any sediment type. The controlling factors are related to the intensity and frequency of disturbance* (Osman and Whitlatch, 1978).

Small, opportunistic tube-dwelling polychaetes are the first faunal components to colonize a new or newly disturbed bottom. Their aggregations may reach densities of 10^5 m^{-2} within a few days to weeks after a disturbance (McCall, 1977; Rhoads, Yingst and McCall, 1978). Tubiculous amphipods appear shortly after the polychaete acme.

Most pioneering species feed near the sediment surface or from the water column. Tube walls to isolate the colonizing organisms from the

sediment, by controlling the rate of diffusion of ambient pore water solutes into the tube environment (Aller, 1980).

An organism colonizing a newly disturbed bottom or new sediment is faced with formidable physiological problems. The pore water chemistry will be unpredictable, especially regarding vertical concentration gradients of pore-water metabolites, metal sulphides, dissolved oxygen**, and organic decomposition products. High concentrations of reduced compounds in the subsurface sediment diffuse across the tube walls and enter the tube interior. Aller (1980) has shown that organisms occupying closely spaced, small diameter tubes efficiently share the work (measured as tube irrigation) required to maintain a constant and low concentration of solutes (e.g. NH_4) in their tubes. The unpredictable chemical and trophic environment below the sediment-water interface may also explain why most pioneering species feed at, or above, the sediment-water interface.

Most pioneering species have adaptive strategies which have been described as r-selected, while many infaunal deposit feeding species share K-selected attributes (McCall, 1977; Rhoads, McCall, and Yingst, 1978). Vermeij (1978) has pointed out that the often cited opportunistic to equilibrium (or r and K selection) end-member classification of benthic marine communities does not represent the full range of possible adaptive types. He recognizes a third end-member called stress-tolerant; species that predominantly inhabit physiologically stressful areas such as the intertidal zone. At this time, the organism-sediment successional model (Figure 1) does not consider this stress-tolerant group of species. However, it is interesting to note that many intertidal species such as Ensis directus (bivalvia) make brief appearances in subtidal pioneering

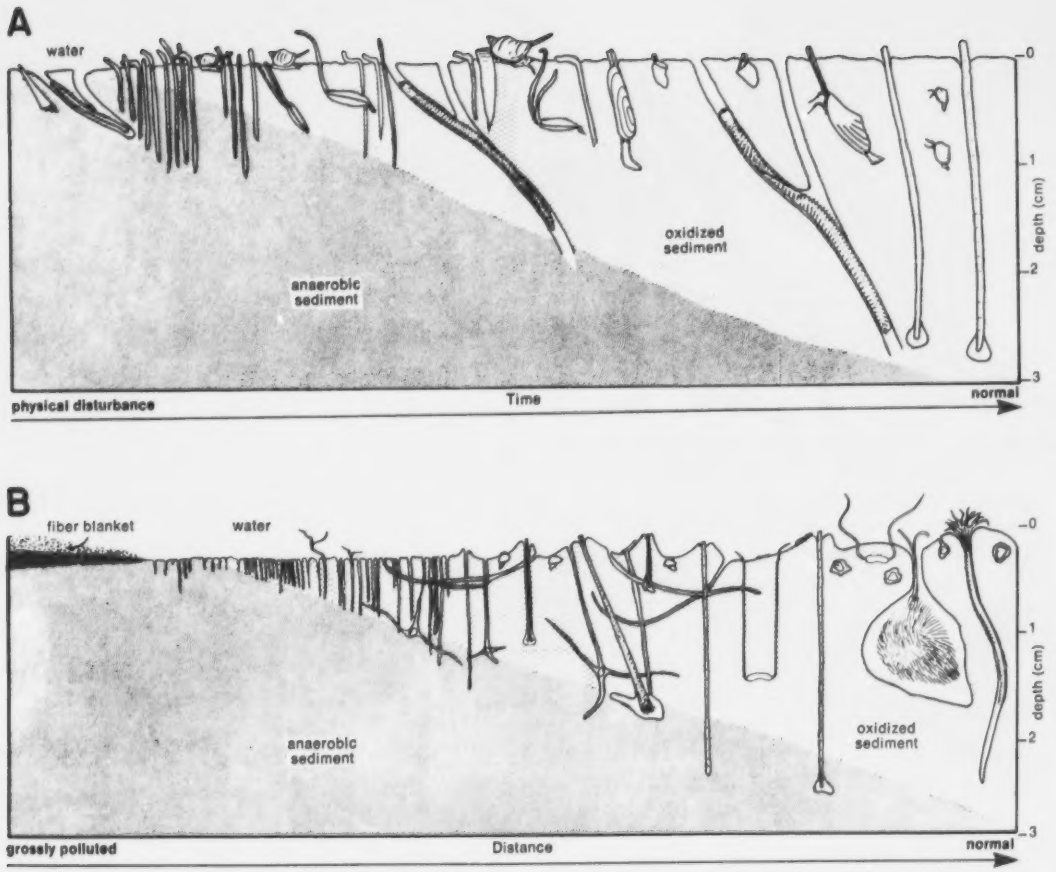

Figure 1. Development of infaunal assemblages over time following a major disturbance (A) and along chronic pollution gradients (B). Pioneering species (left side) tend to be tubicolous or otherwise sedentary organisms that live near the sediment surface and feed near the surface or from the water column. Particle bioturbation rates are low. High-order successional stages (right side) tend to be dominated by bioturbating infauna that feed at depth within the sediment. Particle mixing by bioturbation is intensive. Figure from Rhoads *et al.* (1978a). The pollution gradient diagram (B) is modified from Pearson and Rosenberg (1976).

stages (McCall, 1977).

In summary, the sedimentary effects of pioneering species are limited to the near-surface region of the bottom (§2cm), and they include: 1. Construction of dense tube aggregations which may affect microtopography and bottom roughness on a scale dictated by tube diameter, tube height, and tube spacing. 2. Fluid bioturbation, which pumps water into and out of the bottom through vertically oriented tubes. Particle bioturbation, although present, is of subordinant importance, and, 3. Surface deposit feeding and suspension feeding which cover the surface of the bottom with fecal pellets, especially fusiform pellets of opportunistic polychaetes.

2.2 Equilibrium Stages

High order successional stages are found where major physical disturbances such as intense annual storms rarely affect the bottom. Examples have been described for the Maldanid-Nucula-Syndosmya (polychaete-bivalve) community in the Clyde Sea (Moore, 1931a), the Nucula-Nephtys (bivalve-polychaete) assemblage in Buzzards Bay (Sanders, 1958; Rhoads and Young, 1970); the Molpadia-Euchone (holothurian-polychaete) community of Cape Cod Bay (Rhoads and Young,1971; Young and Rhoads, 1971) the Maldane- Amphiura (polychaete-ophiuroid) community of Ria de Muros, Spain (Tenore et al., in press), and the Lumbrineris-Alpheus-Diolodonta (polychaete-shrimp-bivalve) community in Kingston Harbor, Jamaica (Wade, 1972). A late successional stage is dominated by infaunal deposit-feeders, many of which are represented by 'head-down' conveyor belt feeders (sensu Rhoads,1974). Some of these

species are tubicolous (e.g. the polychaete family Maldanidae) but many others are free living. Equilibrium assemblabes are associated with a deeply oxygenated sediment surface where the redox commonly reaches depths of over 10 cm. Feeding is concentrated at, but not limited to, the redox boundary. The redox boundary is in fact related to the feeding depth*. The redox zone appears to be a region of high microorganism productivity (see Yingst and Rhoads, 1980). Both vertical particle mixing and pore water exchange by respiratory pumping are important bioturbational processes. Organism-sediment relations are complex and well developed in equilibrium systems. In summary, the sedimentary effects of equilibrium species in shallow water environments appears to be: 1. The transfer of both water and particles over vertical distances of up to 10 to 20 cm. 2. Intensive particle mixing produces homogeneously mixed fabrics and many of the particles at, and below the sediment surface may be in the form of fecal pellets. 3. Head-down feeding produces void spaces (feeding pockets) at depth within the bottom. 4. The redox boundary extends over 2cm into the bottom and commonly to depths of 10-20 cm. 5. Surface microtopography may be featureless and planar if tidal resuspension "smoothes" over biologically produced features at the sediment surface, or, in the absence of the smoothing effect, the surface may be covered with numerous feeding pits, and fecal or excavation mounds.

In some cases pioneering and equilibrium species may coexist in the same sediment, if physical disturbance involves only near-surface sediment. Large and deeply burrowed infaunal species may not be affected by such small scale disturbances (e.g. Woodin, 1978). The pioneers may arrive as settling larvae, stimulated by chemical cues associated with the disturbed sediment (e.g. Gray, 1974). I (DCR) have seen mixing of low and

high order successional species in Long Island Sound by the passive wash-in of opportunists from adjacent habitats, but this mixing represents a transient state. Pioneering species may be excluded from equilibrium assemblages by competetive exclusion mechanisms such as trophic group amensalism (Rhoads and Young, 1970). Thayer (1979) has described this phenomenon as biological "bulldozing".

3. Ecological Succession and Geotechnical Properties: A Laboratory Experiment

If sedimentary properties are influenced by the stage of succession, one should be able to observe changes in geotechnical parameters by experimentally introducing the different successional stages into the same sediments, and observing the effects of dominant species on geotechnical properties (see Table I). We conducted such an experiment using sediments and organisms from Long Island Sound (Table I).

A study site called FOAM* is located in 14 meters of water approximately one mile from shore on a mud bottom. This station is maintained in a low order successional stage by seasonal resuspension of the seafloor. Several centimeters of sediment are resuspended during storms (McCall, and Fisher, 1980). The distribution of species at FOAM is patchy, and their abundance and diversity is unpredictable. This high degree of variance arises from the short life spans and high population turnover rates of pioneering species. At best, one may predict that, from the total list of opportunistic species known for Long Island Sound, a small subset of these species will dominate the faunal assemblage at any

Table I. Experimental design of the successional geotechnical experiment

Introduced Macrofauna \ Exp. Tank #	Sediment Source: Station FOAM 1) 1	2	3	Station NWC 2) 4	5	6	7	8	9	10
None (Control)	x					x				x
FOAM Ambient Fauna			x(3)					x(4)		
NWC Ambient Fauna		x(5)							x(6)	
250 Nucula annulata only				x						
49 Yoldia limatula only					x					
25 Nephtys incisa only							x			

(1) 85% silt-clay, $\bar{x}$ grain size = .0125±.0074 mm (N=10)(top 10 cm)
(2) 96% silt-clay, $\bar{x}$ grain size = .0046±.0005 mm (N=20)(top 10 cm)
(3) 6 Nephtys incisa and 4 Clymenella torquata
(4) 3 Nephtys incisa 184 Nucula annulata, 20 Cylichnella canaliculata, 1 Cylichnella oryza plus numerous spionids not retained on the 1.0 mm sieve.
(5) 15 Nephtys incisa, 39 Nucula annulata, 1 Cylichnella canaliculata, 1 Nassarius, plus numerous spionids not retained on the 1.0 sieve.
(6) 3 Nephtys incisa, 107 Nucula annulata, 20 Cylichnella canaliculata, 1 Nassarius trivittatus, 1 Pinnixia sayana, 1 Sipunculida goldfingia(?)?

one time.

Figure 2a shows structural evidence of storm erosion and resuspension of FOAM sediments. A sediment profile photograph (Rhoads and Cande, 1971; Rhoads and Germano, 1981) also shows the density of small tubiculous polychaetes typically present at FOAM (Figure 2b). Some years, the bivalve Mulinia lateralis may arrive as an early pioneer in great abundance. In this case, tubiculous polychaetes are excluded from dense M. lateralis patches (Figure 2c). McCall (1977) has described the faunal dynamics near this sampling station.

Station NWC, locateds in 20 meters of water near the center of the sound, is below the mean shoaling depth of storm waves and supports an equilibrium infaunal community (McCall, 1977; Rhoads, Aller, and Goldhaber, 1977). Three species persistently dominate this station in both biomass and number: the errant polychaete Nepthys incisa, and two protobranch bivalves, Yoldia limatula and Nucula annulata. Figure 3a shows the relatively homogenous sedimentary fabric produced by deep and intensive bioturbation at this station. The sediment surface may be covered with a layer of organic-mineral aggregates (Figure 3b).

3.1 Methods

The successional/geotechnical experiment was set up by bringing defaunated sediment from stations FOAM and NWC into the laboratory. Large macrofauna were removed by passing sediment through a 1mm mesh sieve. Fourteen liters of the sieved mud were placed into each of 10 plexiglass tanks, 36cm long, 27cm wide, and 30cm deep. After settling and compaction, the depth of sediment in each tank was approximately 15cm. Ten liters of sea water covered the sediment in each tank and was

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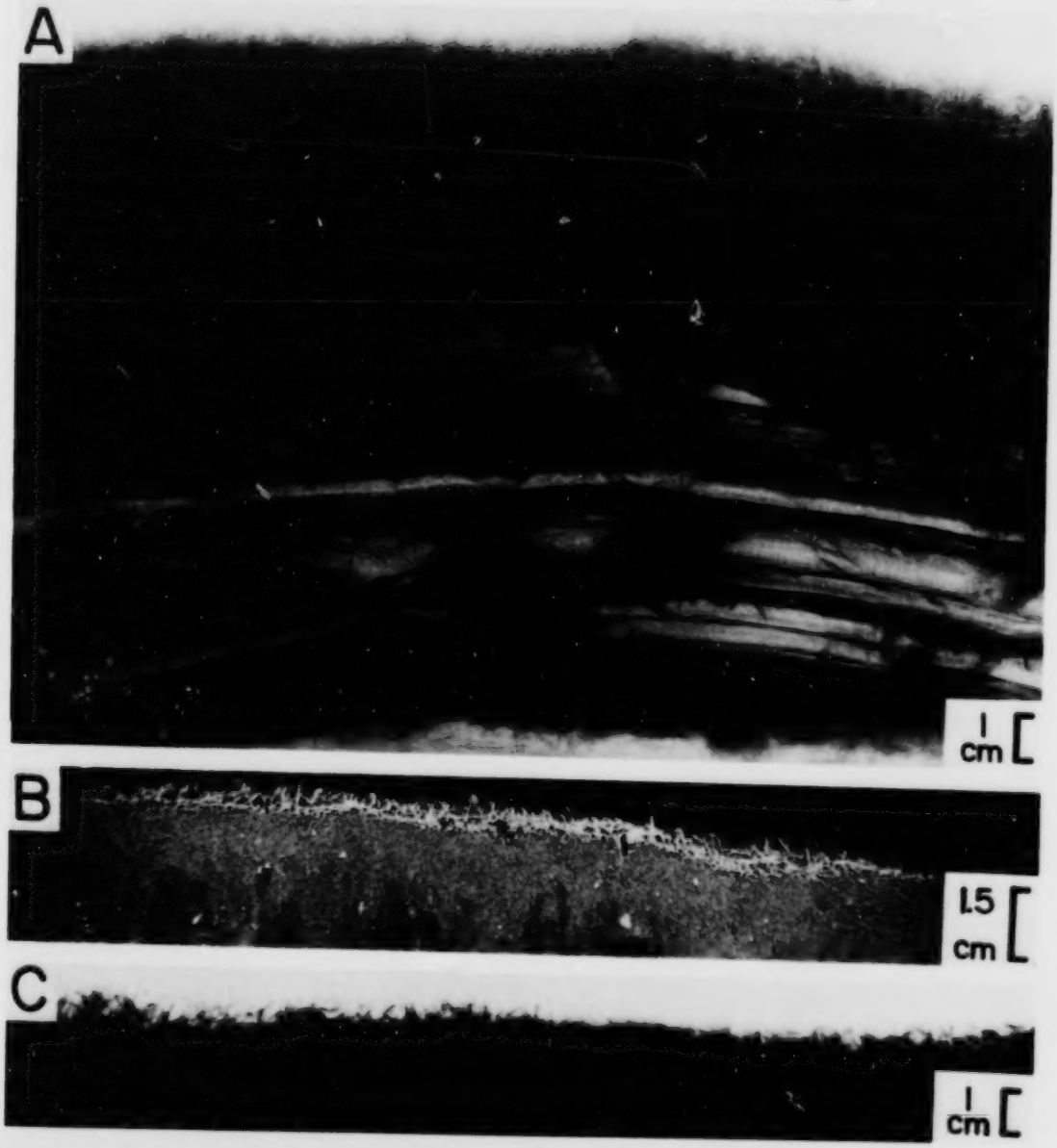

Figure 2. Sedimentary fabrics and biogenic structures in muddy sediments representing a physically disturbed bottom. (A) X-radiograph of station FOAM, showing current laminated sediment lying below a bioturbated interval. Note the unconformity separating these two fabrics. (B) *In situ* sediment profile photograph showing dense populations of pioneering tubicolous polychaetes typically found at station FOAM. (C) X-radiograph of a dense population of the pioneering mactrid bivalve *Mulinia lateralis* also sometimes found at station FOAM.

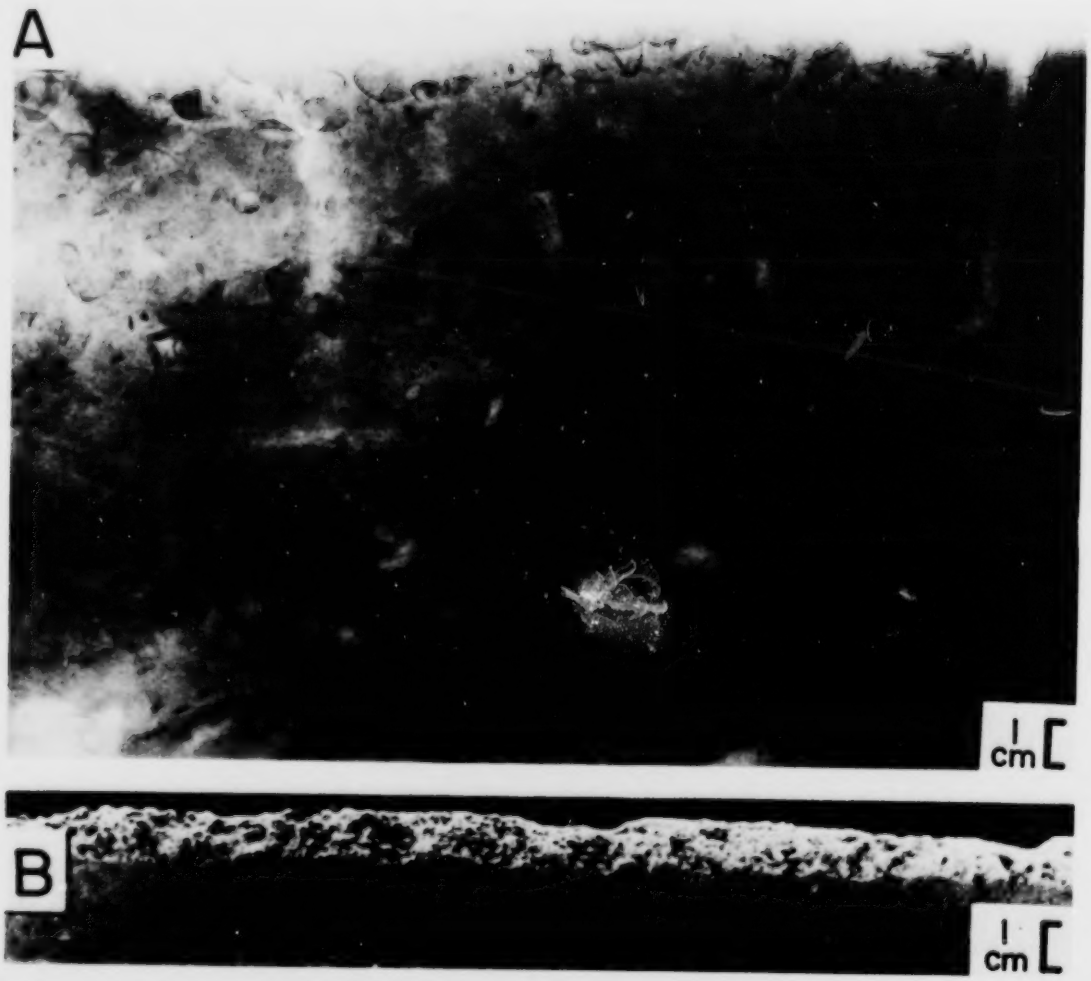

Figure 3. Sedimentary fabrics and biogenic structures in muddy sediments representing a bottom infrequently disturbed by storm. (A) X-radiograph showing the bioturbated fabric typical of station NWC. Note the burrow-mottled structure and random orientation of shells within the sediment. (B) *In situ* sediment profile photograph of organic–mineral aggregates at the sediment surface at station NWC. Note the absence of near-surface-dwelling benthos. Some of the aggregates are fecal pellets; others represent pieces of cohesive surface sediment that have been broken and moved by particle bioturbation.

circulated at 30 liters/hour between the test tanks and a temperature-controlled, 148 liter reservoir. Water temperatures were regulated during the experiment to match the changing ambient water temperature in Long Island Sound (15 to 22 C during the experimental period). Eighteen days after placing sediment into the test tanks, benthic macrofauna were introduced into the test tanks as outlined in Table 1.

Undrained sediment shear strength and sediment water content were measured in each tank over the course of the experiment (57 days duration). Vertical profiles of these two variables were measured at intervals of 2.0 to 2.5 cm to depths of about 12 cm. Water contents were determined by sectioning small cores (2.5cm diameter) and weighing each section (wet wt.) The samples were then dried at 105 C for three days. The sections were weighed, and percent water and water content determined. Shear vane measurements were made with a modified torque screwdriver with specially constructed vanes. The three vane sizes are shown in Figure 4, which relates their breakaway torque to undrained shear strength in muds.

The successional/geotechnical experiment began on July 7, 1980 and terminated on September 2, 1980. Geotechnical measurements were made 13 times over the 57 day period. We report here only data for the beginning and the end of the experiment (day 57). Because of the sediment treatments involved in setting up this experiment (sieving and remolding), and the relatively short term of the experiment, we cannot directly compare field and laboratory values of water content and undrained shear strength from FOAM and NWC sediments. The standards of comparison in this experiment are the controls which lack macrofauna $\pm$ 1mm in size. This experiment addresses the problem of detecting a change in geotechnical

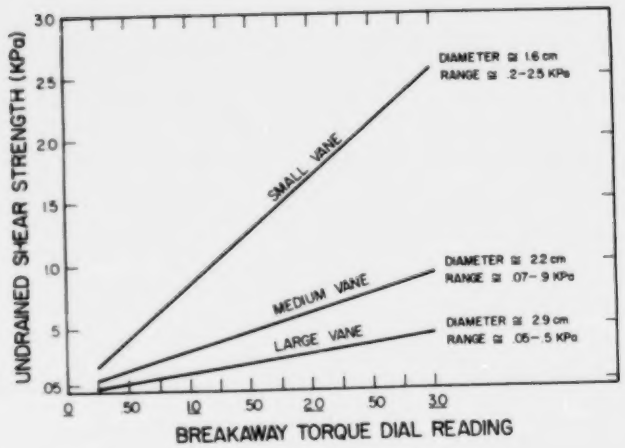

Figure 4. The relationship between shear vane breakaway torque and the undrained shear strengths of our experimental muds. Three vane sizes were used to measure shear strength over the range <0.5–2.5 kPa (1 kPa ≈ 10 g · cm^{-2}).

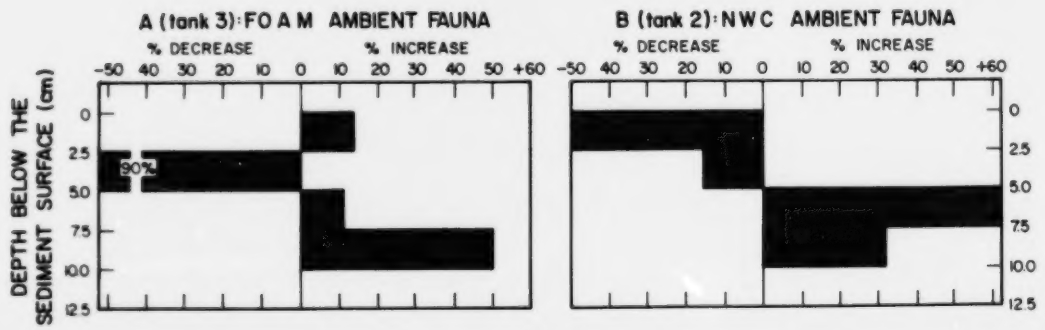

Figure 5. The effects of pioneering and equilibrium species on undrained sediment (mud) shear strengths. (A) Changes in undrained shear strengths of experimental FOAM muds populated with a pioneering macrofaunal benthic assemblage (FOAM). (B) Changes in undrained shear strengths of experimental FOAM muds populated with station NWC equilibrium species. In A and B, plotted values of percent change in shear strengths are relative to a control tank containing FOAM sediment without macrofauna. Shear strength changes shown are for 57 days after introduction of macrofauna. See Table I.

properties relative to the controls. The magnitude of the change can be used to qualitatively estimate the relative effects of pioneering and equilibrium species on geotechnical properties.

3.2 Results

FOAM Sediments - Vertical profiles of undrained shear strength for tank 3 (containing the ambient FOAM fauna), and tank 2 (containing the ambient NWC fauna) are shown in Figure 5a and 5b respectively. The data are plotted as the difference between values measured in the two experimental tanks and values (from the same depth intervals) in the control tank (1). Horizontal bars graphed to the right of the 0 percentage difference datum represent an increase in shear strength relative to the control; values plotted to left represent decreases.

FOAM sediments containing near-surface-living pioneer species experience a 12% increaser in shear strength in the 0-2.5cm depth interval, relative to the control. In comparison, a 50% decrease in shear strength was measured for this same depth interval with the presence of subsurface deposit interval in both tanks shows a decrease in shear strength. This decrease is most dramatic in tank 3 (90%). Radiographs of this sediment show the presence of methane gas voids at depth, which might explain this reduction in shear strength. Methane forms after pore-water sulphate has been depleted. The supply of interstitial sulphate would be expected to be lower in the less intensively bioturbated tank (Figure 5a) compared with the more intensively bioturbated tank (Figure 5b), Below 5 cm, both tanks show an increase in shear strength relative to the control. This depth interval is well below the living depths of the introduced

faunas. Possible "far-field" effects of benthos on sediments will be discussed later.

No difference in sediment water content was observed between the experimental tanks. Surface values ranged from 60 to 61% and declined to about 51% at 15 cm. The shapes of the curves were also similar.

NWC Sediments - Vertical profiles of undrained sediment shear strengths in NWC sediments containing both pioneering and equilibrium species are given in Figure 6a-d. In this experiment two controls were run. The average profile change in shear strength (at day 57) is used as a datum to compare measured changes in the experimental tanks. Tank 4 (Figure 6a) contains the late successional or equilibrium stage bivalve Nucula annulata. This protobranch bivalve has a small, but measureable effect of decreasing shear strengths in the interval 0-2.5 cm. Yoldia limatula, another equilibrium-stage protobranch, has a relatively greater effect in decreasing near-surface shear strengths (tank 5, Figure 6b). Yoldia lives below N. annulata and can burrow to 3-4cm depending on its size. Below the living depths of these two clams, shear strengths increase relative to the controls.

The burrowing depth of the errant polychaete Nepthys incisa depends on its length. In tank 7 (Figure 6c), most of the burrow systems are limited to the upper 3-4 cm but a few large specimens penetrated to 8.5 cm. The effect of N. incisa on sediment shear strength above 5 cm is comparable to that of Nucula annulata (Figure 6a). The increase in sediment shear strength below the burrow penetrated area may represent another "far-field" effect. The decrease in shear strength in the interval 5.0-7.5 cm may be related to the presence of methane gas voids or local influence of a large N. incisa burrow.

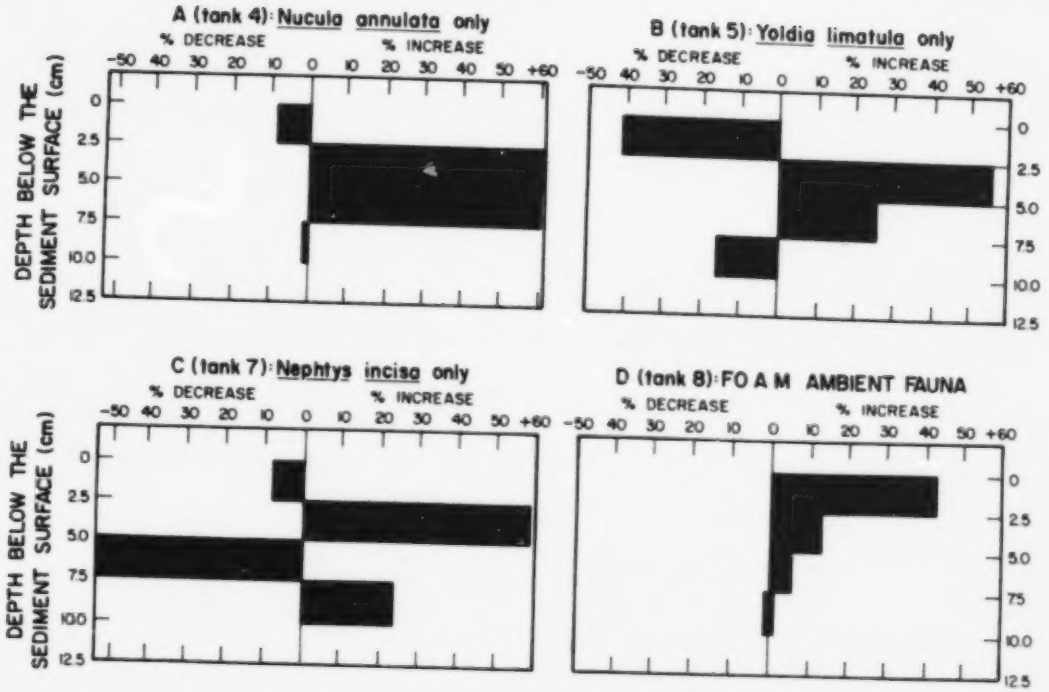

Figure 6. The effects of pioneering and equilibrium species on undrained sediment (mud) shear strengths. (A) Changes in undrained shear strengths of experimental NWC muds populated with 250 bivalves (*Nucula annulata*). (B) Changes in undrained shear strengths of experimental NWC muds populated with 49 bivalves (*Yoldia limatula*). (C) Changes in undrained shear strengths of experimental NWC muds populated with 25 errant polychaete worms (*Nephtys incisa*). (D) Changes in undrained shear strengths of experimenal NWC muds populated with the pioneering FOAM fauna. In A–D, plotted values of percent change in shear strengths are relative to the mean of two control tanks containing NWC sediment without macrofauna. Shear strength changes shown are for 57 days after introduction of macrofauna. See Table I.

Tank 8 (Figure 6d) shows that the ambient FOAM fauna increases sediment shear strength from the surface to 7.5 cm , but that below this depth there is no difference between the test and control tanks. Although FOAM and NWC sediments are somewhat different in organic content and grain size, the addition of pioneering species to these two types of muds results in near-surface increases in shear strength (tank 3, Figure 5a and tank 8, Figure 6b).

Water content profiles of tanks show in Figure 6a-d were not significantly different from one another, nor did they differ from those reported from the FOAM sediment experiments.

3.3 Conclusions

The geotechnical experiment has shown that the successional stage can have an important effect on sediment shear strengths. Within the 0-2.5cm surface interval, particle advection and burrow excavation associated with equilibrium species "dilates", "fluffs", or otherwise decreases the shear strength of the surficial sediment. Although not measured in this experiment, equilibrium species are known to intensively pelletize sediment (Rhoads and Young, 1970; Young, 1971). This pelletization effectively increases the modal grain size of the sediment, reducing the number of particle to particle contacts, and increases sediment porosity.

Pioneering species, as described earlier, live and feed near the sediment surface and are not effective in mixing sediment. When produced, pellets are deposited on the sediment surface. The numerous spionid polychaetes present in the FOAM assemblage pump water into and out of the

sediment through their tubes. This irrigation may stimulate near-surface populations of microorganisms and meiofauna*. The apparent increase in sediment shear strengths associated with this assemblage may be related to mucus binding of particles (e.g. Martin and Waksman, 1940; Frankel and Meade, 1973). The presence of the tubes also increases sediment resistance to horizontal shearing forces. The most interesting results of these experiments are the most difficult to interpret. Every experimental tank showed an effect below the living depths of the introduced macrofauna which we have called a "far-field" effect. We are cautious in our interpretation of these apparent effects.

One would need to repeat this experiment with more control tanks to better evaluate sources of variance in the data. However, we believe that many of the observed "far-field" phenomena may represent real biological effects. Rowe (1974) has shown that burrowing anemones can affect sediment shear strengths as far as 20 cm away from the burrow and tube. Aller (1978) has shown that microbial ATP and production and consumption of decomposition products in the sediment are affected well below the sediment actually occupied by Yoldia limatula. In this case, the far-field effect is related to how the clam influences the rate of exchange of pore-water constituents such as ammonium and sulphate. Bioturbation, especially respiratory pumping, affects the rates of chemical reactions as well as the concentration gradients of dissolved compounds in pore water.

Another far-field effect is related to the depth of the redox below the sediment surface. Respiratory pumping can maintain the RPD several millimeters or centimeters below the surface. The RPD usually lies below the zone of living macrofauna. The RPD is a region of intensive microbial

production (Yingst and Rhoads, 1980). It is also possible that the chemical and physical gradients set up by macrofaunal reworking affect both the distribution and activities of interstitial meiofauna. This size class of organisms can also influence the physical properties of sediment (e.g. Cullen, 1973; Boyer, 1980).

A possible "far-field" effect is related to the density or size stratification of detrital particles at the base of the reworked zone. Silt or sand-sized particles with specific gravities $\pm$ 2.0 are reworked through the zone of bioturbation and as a graded bed (Van straaten, 1952; Rhoads and Stanley, 1965; Rhoads and Young, 1970; Cadee, 1979).

An unexpected result of this experiment is that the water content profiles did not track measured changes in sediment shear strength. We offer two possible explanations. First, sediment water content may be insensitive to the biological activity present in our tanks, at least on the time scale of 57 days. FOAM sediments in the field have summer water contents (% water) of between 50 and 60% within the upper 10 cm of the sediment surface (Aller, Benninger and Cochran, 1980), while NWC sediments normally have water contents $\pm$ 70% all year long (Rhoads, Aller and Goldhaber, 1977). Alternatively, our procedures for storing water content cores (7 C for approximately one week), may have resulted in sediment compaction which "erased" differences in water content.

More geotechnical experiments like the one described here are needed to fully evaluate the relationship between succession and sediment geotechnical properties. Separate experiments must be done for muddy and sandy substrata. Sandy sediments may behave very differently than muds under the same bioturbational regimes, as sands tend to compact rather than "dilate" when mixed (Webb, 1969; Myers, 1977a; Powell, 1977).

4. Sediment Transport

Several biogenic structures and biologically mediated changes in sedimentary properties are of potential importance for determining substratum stability: 1. production of bed roughness, 2. increase in modal grain size through the formation of fecal pellets, 3. secretion of mucopoly- saccharides which coat and bind particles to one another, and 4. change in sediment packing, shear strength, and water content. Each of the above factors will be discussed separately and then related to the successional paradigm outlined earlier.

4.1 Bed Roughness

Organisms produce pits and depressions on the seafloor related to burrowing and foraging activity. Benthos also produce elevations such as mounds from burrow excavation, tracking, and feeding (Frey, 1975). The length scales of these features range from meters (ray pits), to decimeters (shrimp mud mounds) in diameter, and on down to submillimeter scales in the case of fecal pellets deposited on the sediment surface.

Not all bioturbational activity results in an increase in bed roughness on scales of centimeters. If most of the species are small and mobile, the surface may be homogeneously reworked resulting in a very "smooth" and flat bottom. An example of this is described for the mud facies in central Buzzards Bay (Rhoads and Young, 1970). However, if the reworking species are large and relatively sedentary, each individual may

generate considerable topographic relief by its localized feeding activity. An example of this local topographic effect is described for central Cape Cod Bay, Massachusetts related to the presence of mounds made by the holothurian Molpadia oolitica (Rhoads and Young, 1971) and for burrowing shrimp mounds in Discovery Bay, Jamaica (Aller and Dodge, 1974).

Another commonly encountered and qualitatively important biological-roughness-element consists of tubes which project a few millimeters above the bottom. These tubes may be constructed of parchment-like organic material or mucus-cemented sediment grains. Polychaetes and amphipod crustaceans commonly form dense aggregations of tubes in physically disturbed habitats. The spatial scales of the aggregations range from several thousand m^{-2} (e.g. Fager, 1964) to approximately 10^5 m^{-2} (e.g. Eckman, 1979). Tube populations may develop very quickly following a disturbance through larval settlement, reaching densities of 10^5 m^{-2} within a few days (McCall, 1977). These tube fields are usually short-lived phenomena lasting two years or less, as the tube-forming species are subject to mortality from intensive predation (Fager, 1964), or competitive amensalistic interactions with burrowing species (e.g. Myers, 1977). As we will see later, individual tubes themselves may enhance bottom erosion, resulting in eventual wash-out of the population (Eckman, et al., 1981). On the other hand, some tube fields and their associated benthic communities may be relatively permanent; sediment-stabilizing species coexisting with sediment-destabilizing species (Wilson, 1979).

Inferences about the influence of tube fields on substratum stability are largely based on the association of dense tube aggregations with increased topographic elevation of the bottom, a decrease in mean grain

size, an increase in the quantity of organic-rich detritus settling between tubes (Mills, 1967, 1968; Myers, 1977a; Lynch and Harrison, 1970; Featherstone and Risk, 1977; Bailey-Brock, 1979), or absence of traction bed forms within tube fields (Fager, 1964). Indirect inferences about habitat stability have also been based on diversity patterns. Tube patches have a higher abundance and diversity of non-tube constructing species living within them than is found on the adjacent seafloor lacking tubes (Woodin, 1978; Wilson, 1979; Bailey-Brock, 1979; Eckman, 1979).

A extensive fluids literature (see review by Wooding, 1979) exists on roughness elements, however, few flume experiments have been conducted on the effects of animal tubes or other biologically produced roughness elements on substratum stability. Rhoads, Yingst, and Ullman (1978) did flume work with the capitellid polychaete Heteromastus filiformis and showed that three days after a population was introduced into a mud the critical erosion velocity was increased by 80% relative to the critical velocity required to entrain tube-free sediment. The mechanism of sediment stabilization in this experiment is difficult to interpret, because the authors also demonstrated, in a separate set of experiments, that bacterial mucus films can increase entrainment velocities up to 60%. The H. filiformis study did not separate tube effects from microorganism effects. This study also reported an apparent decrease in critical erosion velocity for muds in central Long Island Sound associated with the appearance of a dense set of the polychaete Owenia filiformis. Again, the correlation between the presence of tubes and sediment stabilization does not allow one to identify a simple cause and effect relationship, because the effects of microbial binding were not measured.

While there is only one experimental study of the natural tube

problem *per se* (Eckman et al., 1981), there are many experimental studies of the effects of roughness spacing in flow resistance. The original study was carried out by Schlichting (1936) (c.f. Morris, 1955, Sayre and Albertson, 1963; Lettau, 1961; and Raupach, 1981). Of particular interest is a study by Nowell and Church (1979), for they presented not only resistance diagrams, but also detailed velocity field and turbulent flux profiles. They investigated the effect that different densities of boundary roughness elements have on the shape of the velocity, kinetic energy, and turbulent energy dissapation profiles measured over the total boundary layer. The roughness elements used in their experiments were "Lego" construction blocks. The density of the blocks was expressed as a ratio of the plan area of N roughness elements (blocks) to the total bed area of the flume channel.

At low densities of blocks (less than 1 unit area of blocks / 22 unit areas of flume bottom), each block acts as an isolated element. Turbulent vortices are shed from individual roughness elements and the turbulent energy is transfered to the bed. The kinetic energy and energy dissapation functions show the characteristic monotonic increase all the way to the wall, which is hydraulically rough. At intermediate densities (1/16-1/22), the profile of kinetic energy is approximately constant over a distance of 1 to 2 roughness heights. At the highest densities (1/8 to 1/12), maximum turbulent intensity and the rate of turbulent energy dissapation was elevated to near the tops of the roughness elements, which "protected" the bed within the tube field from higher energy turbulence ("skimming flow" *sensu* Morris, 1955).

The Nowell and Church (1979) study has important implications for predicting how the substratum might respond to the spacing and size of

biological features projecting above the bed. Using the 1/12 ratio as a threshold roughness spacing for initiating skimming flow, Eckman et al. (1981) have shown that natural densities of tubiculous species span the inferred range of stabilizing densities (Figure 7). Of particular interest is the prediction that densities of Owenia reported by Fager (1964) to stabilize a sand bottom from wave surge should destabilize the bed (i.e. give values for crtical shear velocity lower than predicted by Shields curve). Average densities reported by Fager (1964) actually destabilized sediment in the Eckman et al. (1981) flume study. The cause for disparity between Fager's field observations and the Owenia flume experiment is unknown but Eckman, et al. (1981) suggest that the difference between the field observations and their flume experiments is related to the presence of sediment-binding exudates from surface-living bacteria, diatoms, or a commensal anemone which is attached to the Owenia tube.

Changes in substratum elevation, sediment quality, and grain size which are frequently cited as evidence for tube stabilization of the seafloor must be interpreted with care. Even though the tube density falls within the destabilizing region of Figure 7, the bed may be stabilized by exudates of chemautotrophic microorganisms or diatoms. The presence of tubes may be directly coupled with these exudates. Microorganism productivity is enhanced through the increased supply of dissolved nutrients pumped across the sediment-water interface through tubes (Webb, 1969, Aller and Yingst, 1978; Aller, 1980).

Tube fields which fall well within the stabilizing region of figure 7 may still be susceptible to scour and erosion, especially at the leading edge and sides of a patch where flow accellerations occur. In a

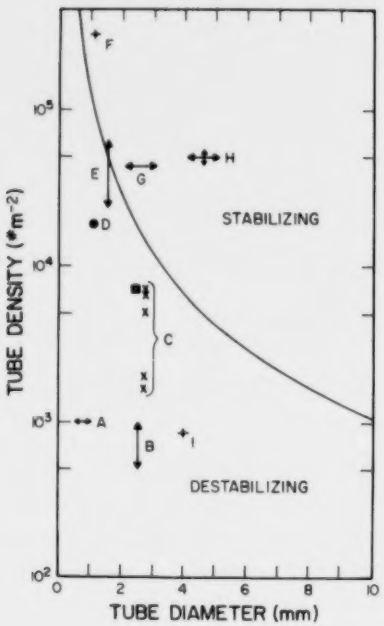

Figure 7. The relationship between tube diameter and tube spacing in affecting noncohesive bed stability. Tube values in the stabilizing field are proposed to initiate "skimming flow," which protects the bed from turbulence. Tube values in the destabilizing field cause bed scour by reattachment of wake turbulence. Modified from Eckman *et al.* (1981). (A) McCall and Fisher (1980) (oligochaetes); (B) Fager (1964) (*Owenia fusiformis*); (C) Eckman *et al.* (1981) (*O. fusiformis*); (D) McCall (1977) (*Streblospio benedicti*); (E) Bailey-Brock (1979) (*Chaetopterid* polychaetes); (F) Myers (1977a,b) (*Corophium insidiosum*); (G) Mills (1969) (*Ampelisca abdita*); (H) Fager (1964) (*Owenia fusiformis*); (I) Myers (1977a,b) (*Microdentopus gryllotolpa*).

rotational tidal current, all sides of a patch may be subject to scour. Most flume and field studies have not addressed the problem of form drag associated with tube patches. Whether "skimming flow" is actually induced by tube dwelling organisms is still unanswered, as flume work has not yet been done with tube densities predicted to be stabilizing (Figure 7).

Another biogenic factor that can armour or protect sediments from erosion is the presence of dense concentrations of shell material at the sediment-water interface. The quantity of shell at the sediment surface is related to both the sedimentation rate and the shell production rate. Pioneering assemblages are highly productive systems, and opportunistic bivalve molluscs (e.g. species of the families Mactridae, Tellinidae, and Pandoridae) may appear in abundances of $10^3 - 10^4$ m^{-2} (McCall, 1977; Rhoads, Yingst, and McCall, 1978). These clam populations usually persist for less than one year. As the death assemblage accumulates, the disarticulated valves may be packed so densely that they armour or pave the interface (Figure 2c).

Sediments may be destabilized by bed roughness produced by surficial tracks and trails. Nowell, Jumars, and Eckman (1981) have conducted flume experiments to determine the threshold velocity for very fine sand tracked by a small (approximately 4 mm) clam, Transenella tantilla. The critical shear velocity was reduced 20% from that of the untracked sediment (Figure 8b). Boyer (1980) has also observed decreases in critical flume entrainment velocities related to the presence of tracks and trails of small macrofauna as well as meiofauna which fluff-up the interface (Figure 9). Although macrofaunal and meiofaunal bioturbation can erase or otherwise reduce the topographic relief of tracks and trails (Cullen, 1973; MacIlvaine and Ross, 1979; Boyer, 1980), meiofaunal

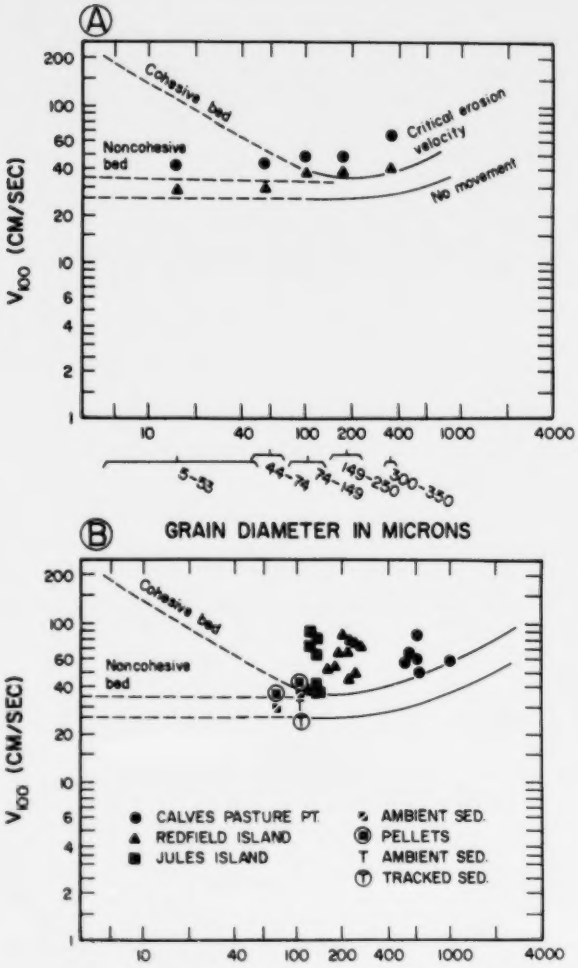

Figure 8. Competency diagrams showing the effects of biological activity on critical threshold velocities. (A) The maximum observed change in mean rolling velocity of five glass bead beds following exposure to microbial growth (replotted from Ullman, 1975). Flow data coverted to z = 100 cm and plotted on a competency diagram. Triangular symbols are initial (aseptic) bead values; circles are values after microbial binding. Microbial binding displaces threshold values above the quartz critical erosion velocity boundary. From Rhoads *et al.* (1978b). (B) Effects of fecal pellets, tracks, and exudate binding on natural sediments. Data on Calves Pasture Pt., Redfield Island, and Jules Island, Barnstable Harbor, Massachusetts, from Boyer (1980). Other data from Nowell *et al.* (1981).

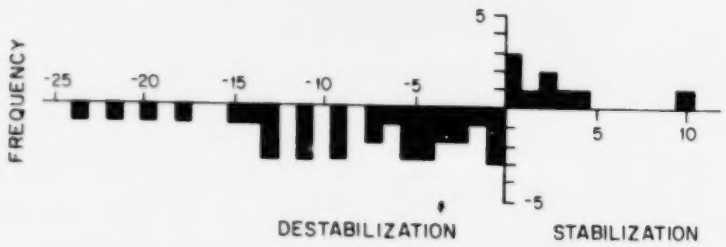

Figure 9. Change in critical threshold velocity for initiating bed movement in fine sandy intertidal sediments reworked by meiofauna. Horizontal scale is change in flume velocity ($cm \cdot sec^{-1}$); vertical axis is measurement frequency. Of the 41 flume runs, 78% ($N = 32$) showed that particle bioturbation lowered the critical velocity. The change in critical velocity is relative to a recently eroded bed surface. From Boyer (1980).

reworking produces a smaller scale boundary roughness on the order of 1mm or less (Grant, Boyer, and Sanford, 1982). In our flume experiments, we have found that ostracods, copepods, and foraminifera moving horizontally just below the sediment surface are effective in producing a characteristic "hummocky" relief to the surface. Grant, Boyer, and Sanford (1982) show that meiofaunal roughening of the bed may lower the critical shear velocity down to near predicted Shields' values.

4.2 Pellet Textures

Much of the potential food for detritus-feeding invertebrates is associated with sediments with high proportions of particles within the silt-clay size range (Sanders, 1962; Purdy, 1964; Whitlatch, 1976). The high surface-area-to-volume ratios of small particles provide a large surface area for the attachment and growth of microbial populations that produce mucopolysaccharide exudates (Zobell,1943; Lynch and Cotnoir, 1956; Hobbie and Lee, 1980). The size fraction of particles selected in the feeding process varies between species. Many deposit feeders preferentially select particles larger than 10 micrometers (Whitlatch, 1976) and below a size of 1mm (Rhoads and Stanley, 1965). In addition to ingesting organic-mineral agregates, relatively 'clean' mineral particles may be ingested and stripped of adsorbed or absorbed organic films (Sulanowski, 1978; Pinck, et al., 1954). Particle selection may also be based on grain density and surface texture (Self and Jumars, 1978; Taghon, et al., 1978).

In addition to the size specificity of food particles, much of the

potential food for detritus-feeding invertebrates is located within the upper few centimeters of the seafloor. In the intertidal zone, useable organic material may be present to a depth of 20 cm (Johnson, 1977; Sulanowski, 1978) and within the upper 2 cm of subtidal coastal sediments (Johnson, 1974, 1977). The above generalizations are based on detailed analyses of vertical profiles of particle morphology, organic content, and total protein and carbohydrate in marine muds and sands (Johnson, 1974, 1977; Whitlatch, 1977, 1980). Detritus feeding is therefore concentrated within, but not limited to, these depths.

With few exceptions, marine benthic invertebrates produce fecal pellets* and these pellets or castings are deposited at, or near, the sediment surface. This generalization also holds true for head-down conveyor-belt feeders which may ingest particles at depths of 20 cm below the surface. Ingested material is usually transported upward through the digestive tract and egested at the sediment surface. In equilibrium communities, these pellets may be subsequently advected downward by bioturbation and distributed throughout the bioturbation zone (Rhoads, 1967). Pioneering species are less efficient in vertical mixing, therefore, pellets remain near the sediment surface. Pelletization may result in a change in the grain size of surface sediments. In muds, this process commonly involves the addition of a very fine pelletal sand fraction to an unpelletized silt-clay matrix (Rhoads and Young, 1970). Because many detritivores preferentially select for particles within the silt-clay fraction, sand-sized fecal pellets are avoided until they break down and the constituent particles are repopulated by algae and/or microbes (Fenchel, 1970; Levinton and Lopez, 1977). Most fecal pellets are produced by the resident benthos, but Moore (1931) describes pelletal

muds from the Clyde Sea that are composed predominantly of zooplankton feces.

Jumars, Nowell and Self (1981) have modelled the fates of sediments which contain deposit-feeders. Their Markov model involves the probabilities of particle selection, pellet disintegration, burial, and the probability of transport of pellets versus "free" unpelletized sediment. The authors show how the steady state abundance of a given particle type comprising a pellet, is a function of pellet durability and particle (feeding) selectivity. High densities of a given particle type in surface sediments result from packaging of particles into durable fecal pellets.

The distribution of pellets in the sediment column depends on their chance burial and preservation. Burial may be by a net input of 'new' sediment or downward advection by particle bioturbation.

Particle residence times are also affected by the feeding types present (Jumars, Nowell, and Self (1981): surface deposit-feeders only (SDF), subsurface deposit feeders only (SSDF), or co-occurence of both of these feeding types (B). Particle residence times are also sensitive to the relative erodibilities of pellets compared to unpelletized sediment.

The production of very fine sand size pellets from silt-clay sized particles would, a priori, appear to favor selective transport of pellets relative to unpelletized sediment. The threshold shear velocity for entrainment of fine sand is lower than that for cohesive silt and clay. Flume observations in natural sediment containing organisms, however, show that pellets do not always have lower critical shear velocities than silt or clay, and may have higher critical shear velocities (Figure 8) (Nowell, et al., 1981). In nature, it is probably a

rare phenomenon to have single, discrete particles of fine sand or smaller grain sizes move independently of other particles. Most particles below fine sand size are associated with organic-mineral aggregates (Rhoads, 1973; Johnson, 1974), held together with microbial mucus (Rhoads, 1973).

Existing competency curves are of limited use in predicting the stability of natural fine-grained sediments because their use is restricted to the particular apparatus or experimental location chosen. Moreover, hydraulic engineers avoid biological growth in their flume channels by adding growth inhibitors to the water. It is not surprising then, to expect major departures in threshold velocities of natural sediments from those predicted by 'azoic' competency diagrams (Boyer, 1980). However, biologically reworked intertidal sediments fall well within the predicted values from the Shields curve (Shields, 1936; Madsen and Grant, 1976; Grant, Boyer, and Sanford, 1982). The Shields curve takes into account the important fluid and sedimentary parameters, to provide the ratio of dimensionless shear to a particle Reynolds number. This curve allows one to compare similar measured grain sizes and fluid shear stresses irregardless of flume design. Moreover, laboratory results can be compared with field measurements or estimates (see Madsen and Grant, 1976).

Nowell, et al. (1981) have conducted flume studies on the threshold velocities of polychaete and bivalve pellet and castings in natural and artificial sediment. Individual pellets, as well as mounds of fecal castings, were held together and to the bed by "elastic" mucus. These pellets and castings were abraded <u>in situ</u> by greater than critical shearvelocities. Mucus cemented individual pellets and fecal mounds to the bottom (Figure 8). Boyer's (1980) flume observations of intertidal

sediments support these observations. The most transportable feces are those produced by species that eject their pellets several centimeters into the water above the bed. Pseudofeces may also be forcefully pumped into the water column (Rhoads, 1963).

The transport of pellets appears to be largely controlled by the presence of binding microbial, meiofaunal, or diatom mucus (excluding algae). Below plant "photosynthetic compensation depth", microbial and meiofaunal exudates are probably the major binding agents. Microbial binding of medium sand to coarse silt-sized, spherical, glass beads has been shown to increase critical entrainment velocities by as much as 60%* in the Rhoads' flume (Figure 8). The onset of a mucus binding effect, starting from initially sterile glass bead surfaces, was observed to be as short as 3 days in laboratory flume experiments (Rhoads, Yingst, and Ullman,1978).

In nature, bacterial colonization of surfaces is enhanced by the adsorption of glycoproteinaceous films onto surfaces (Baier, 1973). Organic films can be adsorbed onto sterile and clean surfaces emersed in sea water within a period of 10 minutes (Goupil, et al., 1973). Clay minerals bear net negative surface charges, promoting the rapid adsorption of mucopolysaccharide films (Khailov and Finenko, 1970). Microbial recolonization of newly produced pellets may take place within a few hours in the summer (Yingst, personal communication). In the absence of intensive particle bioturbation, iron hydroxide encrustations may also serve to bind surface sediments (Parthenaides and Paswell, 1970). Subtidal carbonates, not subjected to bioturbation, may lithify <u>in situ</u> by precipitation of cements. This condition has been proposed to explain the abundant flat pebble (carbonate) conglomerates observed in Cambrian

strata (Sepkoski, in press).

In our flume work with Long Island Sound muds, we have rarely seen individual pellets roll along the bed. As velocity is increased, organic-mineral aggregates** (including pellets) that project above the bed start to vibrate and rock in place.

We have called this the critical exitation velocity (Rhoads, Yingst, and Ullman, 1978). This same phenomenon has been described by Nowell, et al. (in press) for fecal mounds of polychaetes and by Boyer (1980) for polychaete and Hydrobia sp. (gastropod) pellets. The excitation velocity can be well above the predicted critical flume entrainment velocity for detached aggregates. The elastic mucus which binds most particles to one another and to the bed only fails when the flow rate is increased well above the excitation velocity*. As pieces of organic-mineral aggregates break away from the bed, they move downstream as traction or suspended load (depending on the density of the detached aggregate and the flow velocity relative to aggregate diameter). These aggregates can be quite large (1-2 mm) and include pellets, pellet aggregates, as well as irregularly shaped detrital particles. With sustained flow, strings of mucus and mucus bound particles are observed on the surface of the bed; one end of the strand attached to the bed while the free end vibrates and "flails" at a high frequency in the turbulent vortices. These filaments represent coiled sheets of mucus, and are probably the "fibrous binding material" observed in broken sediment surfaces in flume experiments described by MacIlvaine and Ross, 1979; Nowell, et al., in press; and Boyer, 1980.

It is important for future experimental flume work to quantitatively measure the binding mucus at the sediment-water interface. This is a

formidable problem. Mucopolysaccharides are a complex and poorly defined group of macromolecules. Quantitative separation from sediments is difficult, as mucopolysaccharides are closely associated with proteins and inorganic salts (Hobbie and Lee, 1980).

Another problem involves characterizing seasonal changes in mucus production and degradation. Yingst and Rhoads (1980) summarized earlier work on soil microbes: soil microorganisms are known to be temperature controlled in their production of polysaccharides (Martins and Craggs, 1946; Harris et al., 1966). Microorganism assemblages in soils produce a range of chemically different binding agents (Aspiras, et al., 1971) which may differ in their biodegradability as well as in the different physical properties that they confer to soil aggregates. The effect of environmental variables such as temperature on the binding of sediment particles by microorganisms may involve the production of agents of different biodegradability (Martin and Craggs, 1946). Aspiras, et al. (1971) found that maximum structural stability of microbially-bound solid aggregates was reached sooner at high temperatures, but was maintained longer at lower temperatures, once maximum stability was reached.

Mucopolysaccharides also appear to be chiefly produced in microaerophilic environments (Mitchell and Nevo, 1964). Therefore, the production of mucus may vary with Eh and the position of the RPD in sediments. Even if one could make quantitative extractions of mucopolysaccharides from sediments, we question the value of such a parameter for predicting the bed response to fluid shear stress. The critical shear velocity may not be simply a linear function of the absolute quantity of mucus present. Once grain-to-grain contacts are

bridged by an elastic film, additional mucus (increasing film thickness) may have only a relatively minor effect on binding strength. To develop a complete understanding of fine-grained sediment transport we must begin to understand the binding of sediments by mucus (Richards, et al., 1974). However, we foresee serious analytical and methodological problems in characterizing biological adhesion.

Some pellets may move as discrete particles. Risk and Moffat (1977) describe the transport of both pellets and pseudofeces of the intertidal tellinid bivalve Macoma baltica from muddy sediments of the Minas Basin, Nova Scotia. Feces are picked up on the flood tide and transported shoreward. These findings are especially interesting, as Boyer (1980) commonly found that intertidal pellets composed of fine sand and exposed during low tide, are tightly bound to the bottom by microbial and algal mucus.

When pellets or pellet aggregates are entrained, they may move as bed load. This can result from high settling velocities relative to their critical shear velocities (Nowell, et al., in press). If the whole bed is suspended into the water column by wave surge, the presence of fecal pellets can increase the settling velocity of pellet-bound mud by two orders of magnitude (Haven and Morales-Alamo, 1972; McCall, 1979).

4.3 Geotechnical Mass Properties

The mass or bulk geotechnical properties of sediments such as density, water content, Atterberg limits (Lambe and Whitman, 1969), and macroscopic shear strength are all influenced to a substantial degree by

benthic organisms (Chapman, 1949; McMaster, 1962, 1967; Webb, 1967; Rhoads, 1970; Silva and Hollister, 1973; Richards and Parks, 1976; Richards, 1976; Bokuniewicz, et al., 1975; Myers, 1977; Boyer, 1980).

The ease with which free living infaunal burrowers move through, and feed upon, sediments is known to be a function of sediment water content and state of compaction (Chapman, 1949). The limiting force with which burrowing infaunal metazoans can displace sediment is determined by the internal coelomic pressures that can be generated by muscular contraction of their flexible and extensible body wall (Chapman and Newell, 1947; Clark, 1964), or hydrostatic pressures exerted by blood or water vascular systems (Nicol, 1967). To facilitate burrowing and feeding, some metazoa, especially bivalves, also liquify the sediment by injecting water anteriorly into the bottom. This causes an instantaneous local increase in pore-water pressure, and the liquid limit of the sediment is temporarily exceeded. At this instant, the organism moves forward into the liquified zone. In sands, this fluidized sediment represents a transient state, as overburden pressure soon causes the sediment to collapse on itself. In cohesive silts and clays, the sediment may remain dilated long after a burrowing organism has passed through or otherwise processed the sediment. This activity is evident from the presence of abandoned burrows and feeding voids. The mass properties of muds, therefore, reflect the cumulative burrowing history to a greater degree than do rapidly consolidating sands. If burrowing organisms are relatively active, a few individuals per unit area of the bottom can have a major impact on remolding and dilating muds*. The effect of burrowers on a specific sediment is related to the rate of burrowing versus the rate of consolidation. In the sense that muds compact less rapidly than

cohesionless sands, the relative effect of burrowing organisms on the bulk density of muds would be expected to be greater than on sands.

Burrowing in muds has the effect of increasing sediment water content (Harrison, Lynch, and Altschaeffl, 1964; Harrison and Wass, 1965; Rhoads, 1970; Rhoads and Young, 1970; Rhoads, 1973). Intensive particle bioturbation, characteristic of equilibrium communities, is associated with fine-grained sediment water contents that are greater than 60 percent, and commonly over 70 percent (Table II). Burrowing also decreases near surface sediment compaction (Bukuniewicz, Gordon, and Rhoads, 1975), and decreases undrained shear strength, as shown in our geotechnical experiments described earlier (section 3.2). Because many pioneering species are not efficient in mixing particles vertically, these bottom types may compact and have water contents § 60%. However, generalizations are difficult to make because the water content will also depend on the frequency and intensity of physical resuspension by currents. Such a "fluid" pioneering bottom has been described for the Ria Arosa, Spain, by Tenore, et al., (in press). These mud bottoms are apparently resuspended quite frequently (more than once a month), and have a water content (percent water) of over 60% in the upper 12 cm.

Rowe (1974) made in situ sediment shear strength measurements in a highly burrowed mud in Buzzards Bay, Massachusetts, and found average shear strengths to be 0.98* kPa (approx. 10 gm cm^{-2}). Located on this burrowed bottom are sedentary anemones (Ceriantheopsis americanus). Shear strengths of the sediment within 20 cm of the anemones increases to 1.83 kPa (18.7 gm cm^{-2}). The mechanisms by which C. americanus and other macrofauna increase sediment shear strengths, or otherwise promote or permit compaction, are poorly understood. In some cases, the cause and

TABLE II. Near surface water contents of muds bioturbated by errant infaunal deposit-feeders.

Location	Water Content (%)*	Depth Interval (cm)	Reference
Buzzards Bay, Mass., USA	>60	0-1	Rhoads & Young, 1970
Cape Cod Bay, Mass., USA	>60	0-3	Rhoads & Young, 1971
Long Island Sound, Conn., USA	>70	0-1	Rhoads, Aller, and Goldhaber, 1977
Ria Muros, Galicia, Spain	~70	0-2	Tenore, et al., in press
Clyde Sea, Scotland	>80	0-6	Moore, 1931

*Weight of water expressed as a percentage of the initial weight of solids plus water.

effect may be obvious, i.e. walled tube structures within the bottom obviously increase the breakaway torque of a shear vane apparatus or impede the vertical penetration of the bottom by a penetrometer or fall cone. Moreover, large tube dwellers may laterally compact sediments several millimeters away from the immediate tube (e.g. Aller and Yingst, 1979). In the case of C. americanus, the mucus shed from the oral crown may have spread over the sediment surface and caused particle-to-particle adhesion.

Other stabilization mechanisms may be less obvious, such as the interactions between macrofauna, meiofauna, and microorganisms. For example, pore water irrigation is associated with enhanced production of microbial populations and their mucopolysaccharide exudates (Webb, 1969). These viscous and elastic-binding mucus secretions, generated by bacteria as well as by macro- and meiofauna, may fill intergranular pore spaces (Frankel and Meade, 1973). Because many geotechnical properties are related to water content, the inferred range of influence of benthic organisms on the rheological properties of sediments is shown in Figure 10.

In order to evaluate how biological changes in mass properties might influence sediment transport, we have examined much of the literature on the erosion of cohesive sediments. This literature does not present a consensus on the relationships between measured geotechnical properties and critical threshold velocities. Richards, et al., (1976) state that, "at present there is not a satisfactory way to predict the critical (fluid) shear stress of a cohesive bed surface or erosion rates as a function of excess strain". In part, the problem is procedural. Intercomparison of data is difficult due to the diversity of methods used

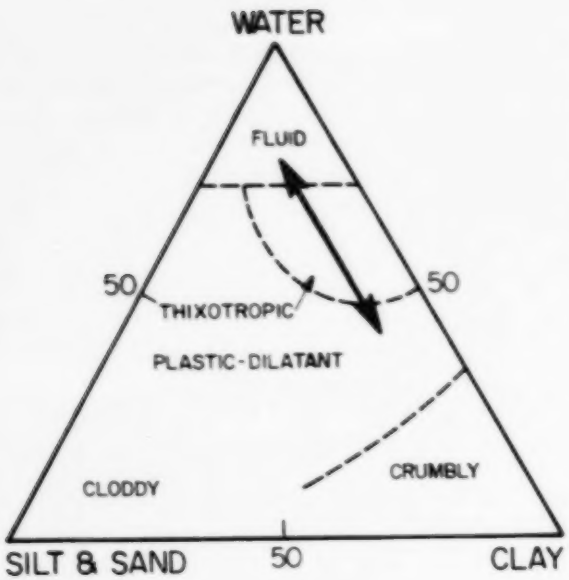

Figure 10. Mass geotechnical properties of sediments related to grain size and water content. In clayey or silt-rich sediments, the properties of the sediment can be significantly affected by the successional stage populating the sediment. The inferred range of effects is shown by the large double arrow. Pioneering species may facilitate the compaction of muds (plastic–dilatant field), but this depends on the frequency and intensity of bottom resuspension by currents. High-order successional species tend to enhance the water content of the bottom through intensive particle bioturbation (thixotropic–fluid field). Diagram modified from Boswell (1961).

to measure geotechnical properties, the range of properties measured, the variety of open and closed channel flumes used, the different criteria applied to identify initiation of motion and mass erosion, and the different manipulation histories and mineralogical compositions of test sediments.

Partheniades (1965), in his review of the literature on cohesive sediment erosion, concludes that shear strength and Atterberg limits are poor predictors of cohesive sediment erodibility. Because incipient bed erosion is related to how fluid shear stress is transferred to the sediment-water interface, one might expect that subsurface geotechnical properties might prove to be uncoupled from processes at the immediate sediment-water interface*.

It is clear that most geotechnical measurements are made on vertical and horizontal scales that are too coarse to adequately address the problem of a natural sediment-water interface. As we have seen in Figures 2 and 3, and described in earlier sections, the biological and physical structure of the sediment surface must be measured and described on the scale of a millimeter or less.

Partheniades (1965) emphasizes the importance of physio-chemical properties of the interface, particularly the configuration and strength of aggregates located at the sediment surface. Although his experiments were done with azoic* clay-rich sediments, his perspective is very relevant to the conditions present on a natural interface composed of mucus-bound organic-mineral-aggregates and fecal pellets. Gularte, Kelly, and Nacci (1980) also suggest that physio-chemical interparticle forces at the sediment surface are extremely important for determining the erosional response of azoic sediments composed of clay minerals.

Some workers have found reasonably good inverse correlations between erosion resistance and sediment water content (Postma, 1967; Southard, Young and Hollister, 1971; Lonsdale and Southard, 1974). Void space, salinity, and sediment shear strength have also been found to be important (Einsele, et al., 1974; Gularte, Kelly, and Nacci, 1980) (Figure 11). Critical flume erosion velocity has been found correlated with the organic carbon content of intertidal sediments (Boyer, 1980; Figure 12). Young and Southard (1979) found the threshold shear velocity for particle movement increased as the Leco carbon content of experimental sediments was increased over the range of 0.8 to 2.0 weight percent. (Organic matter content is correlated with water content (r=.62) in muddy Long Island Sound sediments (Yingst and Rhoads, 1978)).

We previously noted that intensive burrowing and particle bioturbation can produce surface water contents in muds of ↑60% (Table II), and that bioturbation decreases sediment shear strengths. Particle bioturbation would then appear to lower critical shear velocities of muds. Young and Southard (1977) have experimentally shown that U* (critical bottom shear velocity) can be substantially decreased in sediments reworked by errant deposit feeders (Figure 13). Grant, Boyer,and Sanford (1982) indicate that small (§1 mm) macrofaunal and meiofaunal invertebrates, reworking intertidal fine sands, lower the critical shear velocity of previously stabilized sediments.

The flume measurements of Rhoads, Yingst and Ullman (1978) suggest a seasonal change in subtidal mud erodibility in central Long Island Sound over a two-year period (Figure 14). The critical rolling velocity for organic-mineral aggregates ranged from 16 cm sec^{-1} to 28 cm sec^{-1} (velocities calculated for a depth off the bottom of 1 meter). The

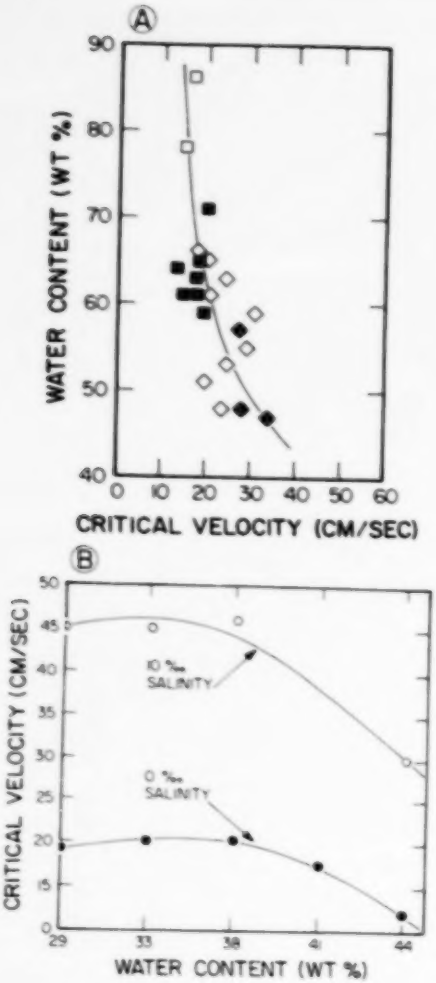

Figure 11. The relationship among sediment water content (weight of water expressed as a percentage initial weight of solids and water), salinity, and critical entrainment velocity. (A) Data from fine-grained shallow and deep-water muds. Velocity given for z = 100 cm. □, From Postma (1967); ◇, from Migniot (1968); ■, from Lonsdale and Southard (1974). Redrawn from Southard (1974). (B) Fine-grained sediment (grundite) erosion as a function of sediment water content and ambient water salinity. Velocity given for closed flume channel. Much of the flocculation between clay particles takes place at salinities ≤10‰. From Gularte (1978).

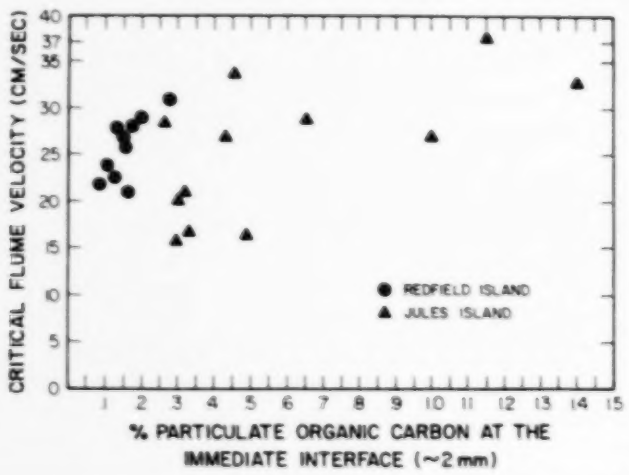
CRITICAL FLUME VELOCITY (CM/SEC)
REDFIELD ISLAND
JULES ISLAND
% PARTICULATE ORGANIC CARBON AT THE IMMEDIATE INTERFACE (~2 mm)

Figure 12. The critical velocity for bed motion in sandy intertidal sediments containing different concentrations of particulate organic carbon at the sediment surface. From Boyer (1980).

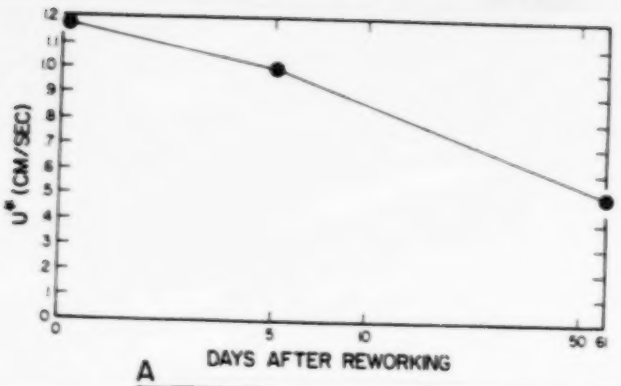

Figure 13. Change in critical velocity ($U^*_{crit.}$) of muddy sediments from Buzzards Bay, Massachusetts, subjected to bioturbation over a period of 61 days. Data plotted from Young and Southard (1978).

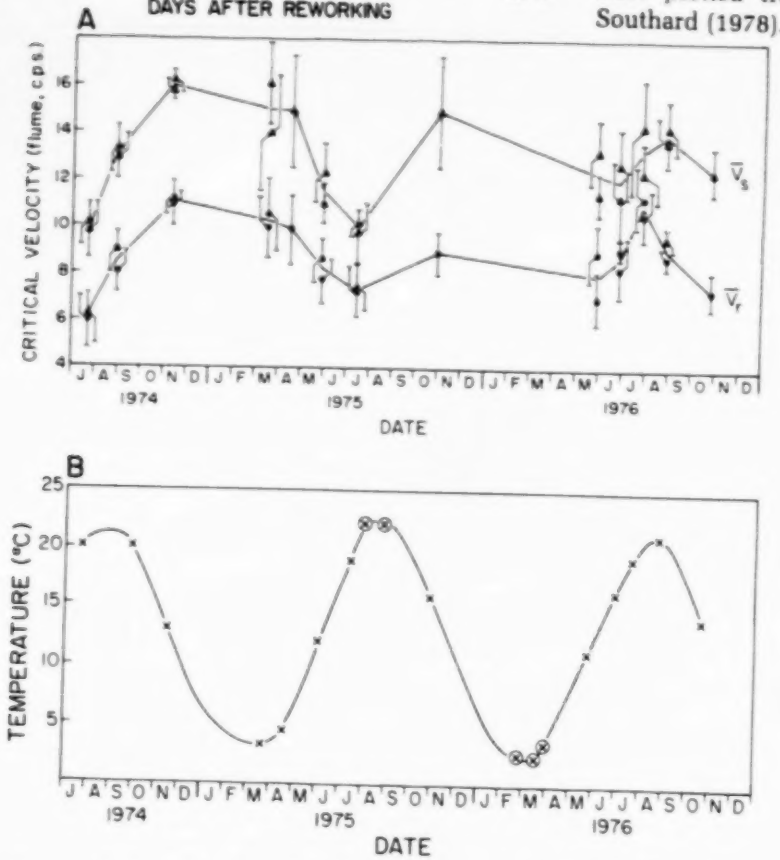
A
CRITICAL VELOCITY (flume, cps)
$\bar{V}_s$
$\bar{V}_r$
J A S O N D J F M A M J J A S O N D J F M A M J J A S O N D
1974
1975
1976
DATE
B
TEMPERATURE (°C)
J A S O N D J F M A M J J A S O N D J F M A M J J A S O N D
1974
1975
1976
DATE

Figure 14. Seasonal changes in seafloor erodibility in central Long Island Sound over a 2½-year period. Measurements made from diver-obtained box cores that were inserted into a laboratory flume. (A) Seasonal change in mean critical rolling velocity and mean suspension velocity at station NWC, central Long Island Sound. Vertical bars represent one standard deviation. Curves fitted to the average of two replicate samples except for April and October, 1975, and October, 1976, when data points were determined from single box cores. Data points are significantly different at the 0.95 level if separated by ≥0.8 velocity units on the y axis. (B) Seasonal change in bottom sediment temperature at station NWC. Circled data points are times when bottom temperatures were taken without sampling with flume cores. From Rhoads *et al.* (1978b).

seafloor was most easily eroded in spring and early summer, and most resistant to erosion in winter. These flume observations are supported by seasonal field measurements of near-bottom turbidity in Long Island Sound (Rhoads and Boyer, in press).

Young and Southard (1977) made in situ Seaflume (a flume deployed on the seafloor; Young, 1977) measurements in Buzzards Bay, Massachusetts, over the period August through February, 1977. The station selected for study appears to be similar to the Long Island Sound bottom studied by Rhoads, Yingst, and Ullman (1978). Young and Southard found U* crit. to vary by a factor of two at measurement sites located only a few meters apart. They attribute this variance to spatial patchiness in unmeasured physical or biological parameters rather than bulk geotechnical properties. No systematic change in U* crit. was detected over the time span of the study. The area of Buzzards Bay where Young and Southard made their measurements was severely affected in 1969 by an oil spill, which killed off many bioturbating species. As of this writing, the equilibrium fauna has still not completely recovered. This fact, plus the relatively short period of measurement, may explain the spatial patchiness in the results of the Buzzards Bay study.

5.0 A Qualitative Predictive Model

There have been two earlier attempts to place organism-sediment relationships into a time-dependent successional framework (Webb, et al., 1976; Rhoads, Aller, and Goldhaber, 1977). We have updated these earlier models in Table III.

The underlying assumptions in Table III are that we are relating

sedimentary properties to end member seres of succession on a subtidal muddy seafloor. A late pioneering stage may be associated with physical properties of the seafloor that are intermediate between the extreme end-member cases outlined in the Table*. These transition states are poorly studied. A second assumption is that the described biological processes are operating at high rates. The effects of seasonality are not considered. In environments with a large temperature range, rates of biological activities may change by a factor of two or more with each 10 C change in temperature. This means that the rate of particle bioturbation by equilibrium species will be dramatically reduced in winter. The physical properties of sediments in late winter may therefore approach 'azoic' values. Fluid bioturbation or irrigation will similarly be decreased in winter. The temperature effect on benthic metabolism is important for explaining seasonal changes in pore water chemistry, and rates at which nutrients are pumped into, and out of, the bottom (Rhoads, Aller, and Goldhaber, 1977; Aller, 1978a, 1978b, 1980; Nixon, et al., 1980; Propp, et al., 1980; Zeitzschel, 1980). If nutrient fluxes are coupled to benthic microbial and mucopolysaccharide production, one might expect a strong seasonal control on sediment cohesion. These interacting factors may be the main reasons for the observed seasonal changes in critical flume entrainment velocities described for Long Island Sound sediments (Rhoads, Yingst, and Ullman, 1978).

Seasonal changes in pelagic primary production, and sedimentation of these products to the seafloor, affect metabolic rates of benthos (Hargrave, 1980). This pulse of organic matter could temporarily increase U* crit. (Young and Southard, 1978). However, U* crit. may decrease if the organic matter is in the form of large aggregates (Riley, 1963), which

are not firmly bound to the bottom. Seasonal changes in benthic primary productivity may be important in determining temporal patterns in the critical shear velocity of intertidal sediments (Grant, Boyer, and Sanford, 1980).

Recruitment patterns of the benthos can also affect rate-dependent processes seen in Table III. Recruitment is often correlated with changes in water temperature and primary production cycles. During recruitment, the density of organisms on the bottom increases by orders of magnitude over long-term, mean abundances. This is especially true of pioneering stages (Rhoads, Yingst, and McCall, 1978). The recruited organisms are all of meiofaunal size (§0.5mm) and occur in a thin zone near the sediment-water interface (Mare, 1938; Yingst, 1978). During the recruitment period there is intensive meiofaunal processing of the sediment surface (Cullen, 1973). Competition between permanent and temporary meiofauna results in high mortality, and abundances of total meiofauna may drop dramatically over a short period of time (Bell and Coull, 1980). In this regard, the muddy seafloor in Long Island Sound is most easily eroded in the spring, a period of intensive benthic recruitment (Rhoads, Yingst, and Ullman, 1978).

We now return to the original perspective of this paper: to make hypotheses about the transport fates of fine-grained sediments and their contaminants. The organism-sediment-fluid interactions outlined in Table III predict that particulate and dissolved pollutants will experience different transport fates depending on the ecological conditions of the seafloor with which they came into contact. For example, a suspended particulate contaminant passing over a pioneering assemblage has a relatively high probability of being intercepted by the numerous

TABLE III. Geotechnical and transport properties of nearshore marine muds as influenced by faunal successional stage. Numbers in parentheses refer to sections of the text where observations and interpretations are discussed in more detail.

PHYSICAL SEDIMENTARY PROPERTIES	Pioneering Stages		Equilibrium Stages	
	OBSERVATIONS	INTERPRETATIONS	OBSERVATIONS	INTERPRETATIONS
1. Shear strength	Increased in upper 0-2 cm interval relative to macrofaunal-free muds (3.2).	May be related to pioneering species pumping water across the sediment surface stimulating surface primary production and microbial growth at the sediment surface (mucopolysaccharide bindingX(4.2-4.3). Slow rate of particle advection allows sediment to compact	Shear strengths in the upper 0-2 cm interval are decreased relative to macrofaunal-free muds (3.2).	Intensive particle bioturbation breaks-up mucus bound surface producing a 'granular' texture at the sediment surface (4.2). Sediment is maintained in a dilated state (3.2).
2. Water content (& density/void ratio correlates)	Depends on frequency and intensity of bottom resuspension by water turbulence	Low water contents (<60%) related to low rate of particle advection. However, frequent bottom resuspension may keep sediment near the liquid limit (4.3).	Commonly >60% in the upper 0-2 cm interval of muds (4.3).	Related to intensive particle reworking and presence of intergranular or interpelletal void space as well as presence of open burrows (4.3).
3. Biogenic texture	Surface pelletized, especially by polychaetes (4.2).	Most particle feeding is done from the water column or sediment surface. Pellets deposited at the surface and are not advected downward (4.2).	Pellets found distributed throughout the actively bioturbated depth interval (4.2).	Most pellets are deposited near the sediment surface but many are advected downward by biogenic mixing (4.2).
4. Surface relief	Patches of densely packed tubes. Patches may be associated with topographic elevations composed of organic-rich fine-grained sediment (2.1-4.1).	Sediment accretion within dense patches (4.1).	Relief depends on species present and their modes of reworking. If species are laterally mobile, relief may be small. If the species are sedentary, the surface may be covered with feeding pits and excavation or fecal and pseudofecal mounds (4.1).	High water content and low shear strength of sediment does not permit topographic relief to develop on a large scale. Relief limited to activities and structures of individual sedentary organisms (2.2-4.1).
5. Sediment transport	Based on observations 1, 2, and 4 above, we predict an increase in $U^*_{crit.}$ at high population densities. At low densities bottom may be destabilized relative to a macrofaunal-free mud (4.1).	Related to mucopolysaccharide binding (4.2-4.3) and/or "skimming flow (4.1).	Based on observations 1 and 2 above $U^*_{crit.}$ decreased relative to macrofaunal-free mud (4.1).	Related to the presence of low density organic mineral aggregates at the sediment surface. Seasonal changes in erodibility may be related to efficiency of mucopolysaccharide binding and rates of bioturbation (4.3).

suspension and surface deposit feeders present. Once the pollutant has arrived at the sediment surface, it also has a higher probability of being ingested and incorporated into fecal pellets. The pellets will be deposited at the surface and may be bound there by mucopolysaccharides, or trapped in stable eddies between densely packed tubes. Dissolved pollutants can come into contact with anaerobic subsurface sediment by being pumped downward 1 or 2 cm through tubes and diffusing through tube walls into the ambient sediment. The residence time of pollutants in a pioneering stage depends on the frequency and intensity of major physical disturbances, which are associated with massive mortality and wash-out of both sediments and fauna. Solid-phase pollutants transported in suspension over an equilibrium community are less likely to be actively filtered or otherwise intercepted by feeding benthos because most of the infauna feed below the sediment surface. However, once a particle settles to the bottom, there is a higher probability that the contaminant will be advected downward, ingested, and incorporated into the deposit in the form of an aggregate. It is also likely that some of the particulate pollutants will reappear at the interface and be resuspended and dispersed by bottom currents with low mean critical shear velocities (e.g. $U^* = 2.0$ for 42um sized particles in Long Island Sound. The resuspended particles may scavenge other dissolved pollutants from the water column (e.g. Aller, 1978; Aller, Benninger, and Cochran, 1980). Dissolved pollutants can be actively drawn into the bottom to depths of 10-20cm by respiratory pumping of burrowing or tube-dwelling species. Muds occupied by equilibrium species are chemically reactive due to intensive particle and fluid bioturbation, and the potential for particle resuspension by weak bottom currents (Aller, 1980). Moreover, the mean residence times of pollutants

in sediments populated by equilibrium communities are expected to be longer than in areas of seafloor dominated by pioneering assemblages.

6.0 Recommendations for Future Work

In order to further test how geotechnical properties of sediments are related to benthic successional history, it is necessary to make *in situ* observations of organism-sediment relations. Conventional means of bottom sampling disturb or destroy important structures near the sediment-water interface*. Free-fall samplers are preceeded by a pressure wave, which washes away small tubes, pelletal layers and fecal mounds. Existing methods of faunal analysis, such as grab sampling and sieving, are similarly inadequate because important information about the vertical stratification of infauna is lost (Rhoads, Germano, and Boyer, 1981). Similarly, the dispersion patterns of tubes and feeding structures, information about surface pellet layers, the depth of the RPD, and the depth of subsurface feeding voids are also lost.

The Rhoads-Cande Profile Camera was developed specifically for the purpose of observing organism-sediment relations *in situ* (Rhoads and Cande, 1971). The ability of this photographic technique to accurately identify successional stages has been documented by Bosworth, et al. (1980) and Rhoads, and Germano (1982). The profile camera technique has been used successfully for over 10 years. We have also found sediment radiography (e.g. Figures 2a & 3a) to provide useful information about sedimentary processes related to the successional paradigm (Tenore, et al., in press).

A newly developed and promising remote sensing technique is that of ultrasound imaging (Orr and Rhoads, in press). Our initial laboratory work has been done with a 1.6 megahertz backscattering system. Small scale (approximately 1 cm) structures can be imaged acoustically at the surface of sediments; more importantly, subsurface structures can be seen to a depth of 10 cm. The ultrasound technique can be adapted to a towed sled vehicle pulled just above the seafloor. Such a system might allow one to rapidly map the distribution of successional stages by providing acoustic information on sedimentary and biological structures at and below the sediment-water interface. At the Woods Hole Oceanographic Institution, Williams and Grant (personal communication) have constructed a 1 megahertz transect monitor capable of measuring topographic changews under waves to 1mm.

High frequency sound may have potential for remotely measuring and detecting changes in mass geotechnical properties (Richardson and Young, 1980). This technique requires inserting an acoustic probe vertically into the surface of the sediment. Sound is propagated horizontally and the difference in travel times along two different path lengths is measured. Vertical profiles in acoustic properties of the sediments can be obtained by sequentially moving the probe downward. This study has shown that bioturbated muds have lower impedance, a lower Rayleigh reflection coefficient, lower bulk and shear modulii, and a lower shear wave velocity propagation than non-bioturbated muds (see Richardson and Young, 1981).

Future work must involve measurement of geotechnical properties on smaller scales than has been done in the past. For problems relating to sediment transport, these measurements may have to be made within one or

two millimeters of the sediment-water interface. We are not aware of any existing geotechnical instruments that can make measurements on this scale.

In situ measurement of critical shear stresses and shear velocity at the ocean floor is also desirable. In this regard, The Seaflume concept of Young (1977) is probably the most appropriate means fort determining the in situ critical shear velocity of natural sediments populated by organisms. In order to better understand complex organism-sediment-fluid interactions, more laboratory flume work is required. Recent advances in forward and backscattering Laser-Doppler Velocimetry technology open up a new approach for accurately measuring water flow and suspended solids within a flume channel. Vertical velocity profiles may be made to within a fraction of a millimeter of the bed without interfering with flow or organisms (Grant, Boyer, and Sanford, 1982). Once again, high resolution profiling is necessary in organism-sediment work because many biological structures and their effects are of small scale.

The influence of tubes, pelletal layers, and mucopolysaccharide binders on sediment stability must be investigated under highly controlled laboratory conditions. Of particular importance is the characterization of mucus binders. This is both a biochemical and a mechanical problem. No one has yet measured the elasticity or breaking strength of these compounds, nor are the kinetics or conditions of its breakdown completely known.

It is clear from our earlier discussion of successional processes and metabolic rate factors that the geotechnical and transport properties of sediments are temporally and spatially dynamic. A sampling program

designed to address the problem of seafloor stability should take into account important biological events. In environments that experience a large annual range in temperature and solar radiation, sampling should be extensive in the spring (when rising temperatures and increasing day length stimulate recruitment and primary production). Sampling in late summer and early autumn will characterize biological processes working at their maximum rates. Early winter is associated with declining metabolic rates and sediment processing. Late winter sampling may closely approximate 'azoic' sediment conditions, as benthic organisms, although present, are metabolically dormant.

Thermally uniform deep water environments may also experience subdued seasonality. Cycles in surface water production result in the sedimentation of detritus to the seafloor in the form of zooplankton fecal pellets (Honjo, 1980). This pulse of detritus may be associated with an increase in benthic activity. In shallow water tropical environments, periodic changes in nearshore salinity and water turbulence during monsoon periods can similarly cause major restructuring of the benthic community.

An areal sampling plan for benthic environs can be more equitably constructed if the physical disturbance history of the seafloor is known, or can be estimated. One need not know this history pricisely. Estimates may be made on the basis of a reconnaissance survey of sedimentary fabrics obtained in x-radiographs of box cores or with an interface camera survey (Rhoads, Germano, and Boyer, 1981; Rhoads and Germano, 1982). The geologist or sedimentologist need not be highly proficient in the identification of benthic species to make judgements about successional history. If the geologist can recognize the functional aspects of benthic communities as outlined in Figure 1, this information is sufficient to

recognize end-member disturbance regimes. Once this organism-sediment information is recorded on a hydrographic chart, the selection of stations for measuring sedimentary or biological properties is facilated.

Aknowledgements

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FOOTNOTES

Page

1. Here defined as the height above and below the sediment-water interface which is occupied, or otherwise influenced, by benthic organisms. The physical effects of organisms extend spatially beyond their immediate "biospace". For example, the current velocity profile, as measured several centimeters away from the bed may be related to topographic boundary conditions controlled by biological features.

Page

2. The term succession has many connotations in the literature (see McIntosh, 1980, for a discussion of the history of the successional concept). We define primary succession as the predictable appearance of macrobenthic invertebrates belonging to specific functional types following a benthic disturbance. These invertebrates interact with sediment in specific ways. Because functional types are the biological units of interest for this study, our definition does not demand a sequential appearance of particular invertebrate species or genera.

Page

3. The example of disturbance used in our review is the physical reworking of the seafloor by waves and currents. This is only one category of disturbance that can restructure benthic communities. For a comprhensive review of the physical, biological, and chemical perturbations that can affect macrofaunal succession we refer the reader to Pearson and Rosenberg, 1978; and Dayton and Oliver, 1980.

Page

4. Mapping the depth of the redox potential discontinuity (RPD) below the surface of marine sediments has proven useful for assessing the affect of organic pollution on the benthic ecosystem (Pearson and Stanley, 1979; Rhoads and Germano, 1981). The cause and effect relationships are complex. In areas of the seafloor experiencing organic enrichment, biological oxygen demand (BOD) and chemical oxygen demand (COD) are highly correlated with organic decomposition. This oxygen demand causes the Eh=0 horizon to rebound toward the sediment surface. The enrichment is also associated with the appearance of pioneering species which are relatively ineffective in exchanging ambient pore water with overlying water, hence the redox remains near the sediment surface.

page

5. The depth of the redox boundary can be visually seen as a brown oxidized layer at the surface of the sediment, or locally around tube and burrow walls. In sediments high in iron content, this colored layer may not, in many cases, reflect the presence of free molecular oxygen in sediment pore-water. Once oxidized, ferric iron may persist long after the associated pore water has been depleted of dissolved oxygen (Revsbech, Jorgensen, and Blackburn, 1979).

Page

6. Station FOAM is located near McCall's (1975, 1977) site A. The FOAM site has been the location of intensive geochemical investigations

and is appropriately named "Friends of Anoxic Muds" (FOAM, goldhaber, et al., 1977).

Page

7. Total meiofaunal and microbial adenosine triphosphate (ATP) at the sediment surface at FOAM is more than twice that at the sediment surface at station NWC (Aller and Yingst, 1980).

Page

8. Pseudofeces, particles manipulated, but not ingested by an organism, may also be ejected or deposited at the sediment surface. Pseudofeces are usually less consolidated than fecal pellets and castings.

Page

9. Alcian blue staining of the glass beads showed the presence of carbohydrate-rich mucus at very small point contacts between grains. These contact films were barely visible under 50x magnification.

Page

10. Many of these aggregates may have their origins from the water column by the formation of particulates from dissolved orgainic matter, adsorbed onto bubble surfaces (micelle formation), or onto other surfaces in the water column (Riley, 1963; Krank, 1973, 1975). When the aggregates reach the seafloor they are mixed into the bottom and become part of the detrital food chain.

Page

11. Using microbially bound glass beads, Ullman (1975) found that the mucus bonds failed after the flume velocity was increase approximately 77% above the excitation velocity. Boyer (1980) also found that mucus-coated, intertidal sands had a "tear-away" velocity approximately 70% higher than the excitation velocity using the same flume.

Page

12.Burrowing may operate together with pelletization to cause sediment dilation. The presence of pellets can decrease packing through the production of interpellet void space.

Page

13. Subsurface mass properties might be more appropriately described for determining the extent of massive bed erosion.

Page

14. Insufficient data are given in most engineering studies to determine whether or not bacterial or plant activity was excluded from the sediments under examination. By "azoic" we mean that no micro- or macroorganisms were deliberately introduced into the sediment at the onset of the experiment.

Page

15. The time involved in a succession such as the one outlined in Table III and in Figure 1 depends on many factors, and is poorly known. Our best estimate is that a primary succession, starting at a macrofaunal free state, will take tens of years to develop into a persistent

equilibrium community. This estimate assumes that the system remains undisturbed in the course of its recovery.

Page

16. The only ship-deployed sampler that I (DCR) have seen that recovers a nearly undisturbefd sediment-water interface sample, is a spade box core, which has been fitted with internal vertical partitions. These partitions dampen-out water motion over the bottom as the sample is recovered (e.g. Hessler and Jumars, 1974).

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